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PHORADENDRON

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Several years ago my attention was seriously called to the need of a revision of our leafy mistletoes through inability to understand the basis of characterization that could admit to one species such different appearing plants as those from the southeastern, southwestern, and arid United States—not to mention California and Yucatan—to which the name *Phoradendron flavescens* is currently applied. Among their manifold differences, a diligent search was made for characters; the types of related species and varieties that have been held to be differentiable from *flavescens* were examined with care, and every form occurring in the United States was traced to the known limits of its range, sometimes south of our national border. As political boundaries do not often form satisfactory limits to such a study as I had begun, I was quickly lured into an examination of the Mexican species which approach our border, and of others which reach into the field of these, so that no arbitrary geographical limit, even, could be fixed short of the Isthmus.

In the course of this study it became apparent that the great conservatism of Engelmann, who seems never to have given this genus the care that marked his study of the related genus *Arceuthobium* or *Razoumofskyia*, had not only caused him to withdraw segregates of *P. flavescens* that he admitted at one time, but had reacted on his early colleague in the study of our southwestern plants, Torrey, to the extent of causing a number of forms which had been designated in the Torrey herbarium as new species to lie there, as they still do, without publication.

At the New York meeting of the National Academy of Sciences, in November, 1911, and at a meeting of the Academy of Science of St. Louis on December 18, 1911, the preliminary results of this study of the northern species were outlined, and this was followed at the Washington meeting of 1912 by presentation to the National Academy of the manuscript of a revision of all of the forms of *Phoradendron* recognized as occurring in continental North America. As I was then on the eve of departing for a year in the great herbaria of Europe, this revision was withheld from immediate publication in the hope that several obscure Mexican species could be cleared up certainly, through authentic specimens, and in the hope that they might be illustrated from the types. Though the admission of Torrey's long neglected manuscript names

had quite prepared me for an apparently inordinate increase in the number of differentiable species in the genus, I was not a little surprised to find, when casting my results then into classified form, that on an average nearly two new named forms appeared for each one already admitted to our flora.

Notwithstanding an intention to limit my investigation to the species of continental North America, the temptation to learn the characters of the South American species proved irresistible when, at Brussels, I examined the specimens in the personal herbarium of von Martius, whose collections have done so much to make known the flora of Brazil; and it was not long before the genus as a whole engaged my attention, though West Indian material was given less care than the other until at Dahlem I reached the collection of Professor Urban, who in 1897 had published a revision of all of the West Indian Loranthaceae. To my keen satisfaction, I then found that for the Antillean region very few forms were to be differentiated from those admitted by Urban, confirming my judgment that the large increase in our own flora rested upon previous neglect of application to them of characters which appear to be really differential, rather than to excessive optimism concerning their separability. The thorough study of tropical forms by Eichler in his revision of Loranthaceae for the Flora Brasiliensis, in 1868, supplemented by a reëlaboration of available material when Urban monographed the West Indian forms, has also prevented an increase in the number of South American species at all comparable with that within our own flora, though the number of names added is relatively greater than for the Antilles.

The essential characters of *Phoradendron* in its group of Loranthaceous genera are chiefly its axillary spikes of sessile unisexual and monochlamydeous small flowers often sunken in hollows of the frequently swollen internodes of the rachis, normally trimerous, with 2-celled longitudinally dehiscent anthers. A very few species, like *P. cymosum*, present the phenomenon of a terminal spike corresponding to the 1- or few-flowered cyme of the old world *Viscum*, but in addition to axillary spikes. Except in the species taken by Hooker for *falcatum*, the receptacular cups, which range from so shallow as hardly to surround the base of the flower to a depth covering a noticeable part of the mature fruit, are essentially even on their margin; but in this species the cup is parted so as to present sometimes the appearance of a deeply divided calyx. The flowers, with a small vestigial nectar-gland and apparently adapted to pollination by such short tongued insects as flies and small bees, are usually yellowish green when expanded, but in *P. Brittonianum* and some of

its relatives the sepals are blood-red even before anthesis. Some species are known to be apogamous and apogamy is to be expected in many others, a circumstance very probably connected, as in *Taraxacum* and *Hieracium*, with polymorphism or close affinity in species as now understood.

In all of our own species the plants are strictly dioecious and, as a rule, staminate spikes are longer than pistillate and bear more flowers. This is known to be true also of a number of tropical species, such as *P. Wattii*: in others, prevailing if not exclusively staminate and pistillate spikes showing something of the same dimorphism occur monoeciously on the same plant. Though usually not too closely applicable as between related species, the number and arrangement of the flowers on a given spike present equally characteristic differences, but with the qualification that flowers of the uppermost joints may be fewer in number and simpler in grouping than below, while one or two of the lower joints may be partly or entirely without flowers, the lowermost almost universally being reduced to a sterile peduncle. The greater number of tropical species differ from those of the north in being androgynous through the occurrence of a number of staminate flowers on spike-joints that are otherwise pistillate, or, less commonly and sometimes differentiated by the term 'gynandrous,' through the occurrence of a few pistillate flowers on otherwise staminate joints,—as many of Eichler's accurately drawn plates show very beautifully. Except in a broad way, these differences do not appear to be practically applicable in contrasting species though representing in part morphological differences of fundamental taxonomic value. The prevailing grouping of the flowers is in 2, 4, or 6 series on each joint of the spike; i.e., in 1, 2 or 3 ranks over each of the two scales by which it is subtended. Examples of the first and last are given by *P. laxiflorum* (2), and *P. flavescens* (6), and where the joints are unisexual these numbers commonly prevail, though four series may be found by reduction and as many as ten by increase when the number is typically six. When the joints are androgynous, the staminate flowers often occur at top between the normal two ranks over each scale, and this condition is usually accentuated on luxuriant spikes and sometimes on all by the downward intrusion of a partial or complete third series over each scale. For the separation of the groups into which tropical species fall, I have found it most convenient to use the prevalence of 2 or 6 series of flowers on the joint as a differential, providing as an intermediate the prevalence of the interjected two series under the designation 4 + 2. A glance at *P. domingense* (2), *P. trinervium* (4 or 4 + 2), *P. hexastichum* (6) and *P. Lindavianum* (6–10) will make these distinctions evident,—

more than 6 ranks being very exceptional except in some tropical species with leaves venulose above and dull beneath, and in some of our northern forms.

One of the characters most available and significant in the classification of the species of *Phoradendron* is a fundamental difference in their leaves. By far the larger number of species have unmistakable leaves, but our western group to which *P. californicum* and *P. juniperinum* belong have their foliage reduced to short thin scales which resemble the leaves of the related genus *Arceuthobium* or *Razoumofskya* so closely that species of either genus are commonly to be found in herbaria as representative of the other. Unlike typical foliage leaves, these scales do not disarticulate, though a constriction at the base of the scales in two forms affords partial ground for their specific recognition: one species of the Mexican mountains, *P. minutifolium*, has almost equally small though fleshy disarticulating leaves, and two of the South American species, *P. tunaeforme* and *P. fragile*, are characterized by bearing small scale-like leaves only. Such species are very likely to be mistaken for some representatives of the related genus *Dendrophthora*, which differs technically in its 1-celled anthers.

If any species of the United States, for example *P. Eatoni* of the everglades of Florida, is compared with any West Indian or South American species, for example *P. rubrum* of the Bahamas, the latter will be found to possess constantly in addition to its foliage one or more pairs of scale-leaves at least on the lowermost foliage internode of every branch. Comparable with the scales of the flowering spikes and with the stem-scales of *P. juniperinum*, etc., these cataphyls afford by their presence or absence what proves to be one of the most important of characters for the primary division of the genus *Phoradendron*. Usually cataphyls do not subtend flowers or spikes, apparently serving no function further than the protection they may afford the shoot in its earliest development; but in *P. crassifolium* and *P. craspedophyllum* spikes are regularly and characteristically found in the axils of some of the cataphyls, and less characteristically in a few other cases.

Never found on any species of the United States, absent from three-fourths of those of Mexico and Central America, but invariably present on all of the South American and West Indian species, these scales are usually confined in the latter to the basal joint of each branch, though in cases of true or cymose forking they are found on all joints—since only basal joints are then present. In a very small percentage, only, of the tropical species with percurrent or monopodial branching, e.g., *P. flavens* and *P. crassifolium* and their allies, cataphyls are found on all

foliage internodes; and in a single known species, *P. paradoxum*, the stem is made up of rather terete joints with cataphyls and ancipital joints without them, in regular alternating succession.

In the geographic distribution of its species, *Phoradendron* is rather unusually instructive. The genus is strictly American and extends from Washington, Colorado, the mouth of the Ohio River, and southern New Jersey to the Southern Argentine region on the continent, and through the entire West Indian chain; one species occurs in the Pacific island Guadalupe, and two are found in the Galapagos group of Pacific islands,—both oceanic but with American floras. None of its many species of fairly homogenous character possesses a very wide geographic range. Marked examples of widespread occurrence are afforded only by a few such polymorphous species as what is usually called *P. latifolium*, or an assemblage of intricately related if differentiable species like that usually known as *P. rubrum* or *P. quadrangulare*, both of which range from Brazil to Central Mexico and well through the West Indies. Few species, indeed, equal in range our native *P. flavescens*, which occurs from southern New Jersey to the lower Wabash, Oklahoma and eastern Texas, reaching southeast to the Gulf and ocean.

Admirably endowed with means of free dissemination through its edible berries with extremely viscid pulp, which leads to their dispersal by birds, these mistletoes seem limited nevertheless to a surprising extent by ordinary barriers to plant migration. Like the similar European *Viscum album*, with its scarce-definable races capable of effective germination only on the host-species from which the seed came, our eastern *P. flavescens* though attacking a large variety of host plants is usually found confined to a single host in a given region, and such experiments as have been made on it show that it can be transferred from one host to another with difficulty if at all. How far this may be concerned in the polymorphism of this species and how far its like may serve to limit the dispersal of most species is at present a matter of conjecture only.

Viewed on broad geographic lines, the species of *Phoradendron* usually occupy areas that present severally an assemblage of fairly uniform meteorologic features with limiting environment,—in this respect agreeing with most other plants and with animals. In the main, the regions affected by individual species of *Phoradendron* are the following:

North America: (1) Atlantic, (2) Rocky Mountain, (3) Pacific, (4) Great Basin or Sonoran,—in the United States; (5) Table-land, (6) Eastern or Western Sierra Madre, (7) Western riparian, (8) Yucatecan, and (9) Cordilleran,—in Mexico and Central America.

South America: (10) Andean, (11) Peruvian and Bolivian, (12) Argentine, (13) Brazilian upland, apparently with less differentiation than would be thought between the arid and humid portions, (14) Amazonian, (15) Cayenne, and (16) Venezuelan.

West Indies: (17) Caribbean, (18) Antillean, to the north of the Anegada passage, and (19) Bahamian.

Few species range throughout any one of these regions, and it is very rare for a species to reach from one into the other.

Briefly summarized, the purely taxonomic part of my study of the genus leads to the conclusion that *Phoradendron* may be best divided into two primary groups, respectively constantly without and constantly with cataphyls on their foliage shoots: for the first I am using the name BOREALES, since its species alone are represented in the north; and for the other, AEQUATORIALES, since its species only are found in the equatorial region. Species destitute of expanded foliage are found in each group in small numbers. Those of the first group are pubescent for the most part, while only two of the second group are more than papillately roughened. The Boreales appear to be strictly dioecious; the Aequatoriales for the most part, though not exclusively, are monoecious, usually with some or all of their spikes androgynous.

So far as shown by the material now contained in the great herbaria at Washington, New York, St. Louis, Chicago, Brussels, Copenhagen, Kew, Munich (where von Martius' official collection is), Geneva, Budapest, Prag, and Dahlem, and in many smaller collections, I find a total of 262 differentiable forms, most of which I regard as species, and of which 60, or 23 percent, are of the Boreales and 202, or 77 percent, Aequatoriales. Of the Boreales, 41, or two-thirds, and of the Aequatoriales, 85, or two-fifths, are characterized as new.

The distribution of the main groups (species which occur in more than one region being included in each) is:

	U. S.	Mexico	Centr. Amer.	W. Indies	S. Amer.
BOREALES.....	26	45	1	0	0
AEQUATORIALES.....	0	25	23	34	124
	—	—	—	—	—
	26	70	24	34	124